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Effects of plant diversity on invasion of weed species in experimental pasture communities

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Summary

Studies have shown that weed invasion into grasslands may be suppressed if the resident plant community is sufficiently diverse. The objective of this study was to determine whether increased forage plant diversity in grazed pasture communities might be associated with reduced weed abundance both in the aboveground vegetation and soil seed bank. Data were collected from a pasture experiment established in 1994 in Missouri, USA. The experiment consisted of 15 m $\times$ 15 m plots sown with *Festuca arundinacea* Schreb. or *Bromus inermis* Leysser as a base species in mixtures of 1, 2, 3, 6, or 8 forage species. The plots were grazed by cattle during each growing season from 1998 to 2002. Aboveground plant species composition in each plot was measured using a point step method. Soil cores were collected in 1999 and 2002, and the species composition of germinable weed seeds in plots were evaluated by identifying seedlings as they germinated over an 8-week period. Species diversity was measured using several indices: species richness (S), Shannon–Wiener diversity index (H'), and forage species evenness (J). Aboveground weed abundance in plots was unrelated to forage species richness (S), but weed abundance declined as the evenness (J) of resident forage species increased in mixtures. The species composition of mixtures may have affected weed abundance. Weeds both in the soil seed bank and aboveground vegetation were less abundant in mixtures that contained *F. arundinacea* compared with mixtures that contained *B. inermis*. Although variables like forage plant productivity may also suppress weed abundance in pastures, our results suggest that maintaining an evenly distributed mixture of forage species may help suppress weeds as well.
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Zusammenfassung

Untersuchungen haben gezeigt, dass die Unkrautinvasion in Grünländer unterdrückt sein kann, wenn die ansässige Pflanzengemeinschaft ausreichend divers ist. Die Zielsetzung dieser Untersuchung war es zu bestimmen, ob eine erhöhte Futterpflanzendiversität in beweideten Grünlandgemeinschaften mit einer verringerten Unkrautabundanz sowohl bei der oberirdischen Vegetation als auch in der Bodensamenbank verbunden sein kann. Die Daten wurden in einem Weidelandexperiment gesammelt, das 1994 in Missouri, USA, etabliert wurde. Das Experiment bestand aus $15\,\text{m} \times 15\,\text{m}$ Probeflächen, die mit *Festuca arundinacea* Schreb. oder *Bromus inermis* Leysser als Basisarten in Mischungen von 1, 2, 3, 6 oder 8 Futterarten eingesät waren. Die Probeflächen wurden während jeder Wachstumssaison von 1998 bis 2002 stark mit Vieh beweidet. Die oberirdische Pflanzenartenzusammensetzung wurde in jeder Fläche mit einer Punktstopmethode gemessen. Bodenproben wurden 1999 und 2002 gesammelt und die Artenzusammensetzung der keimfähigen Unkrautsamen wurde in den Probeflächen bewertet, indem die Keimlinge identifiziert wurden, die in einer 8-wöchigen Periode keimten. Die Artendiversität wurde unter Verwendung verschiedener Indizes gemessen: Artenreichtum (S), Shannon–Wiener-Diversitätsindex (H') und Futterarten-Äquitabilität (J). Die oberirdische Unkrautartenabundanz in den Probeflächen stand in keiner Beziehung zum Futterartenreichtum (S), aber die Unkrautabundanz nahm ab, wenn die Äquitabilität (J) der ansässigen Futterarten in den Mischungen zunahm. Die Artenzusammensetzung der Mischungen könnte die Unkrautabundanz beeinflusst haben. Sowohl die Unkräuter in der Bodensamenbank, als auch in der oberirdischen Vegetation waren weniger abundant in Mischungen, die *F. arundinacea* enthielten, im Vergleich zu denen, die *B. inermis* enthielten. Obgleich Variablen wie die Futterpflanzenproduktivität möglicherweise ebenfalls die Unkrautabundanz im Weideland unterdrücken, lassen unsere Ergebnisse vermuten, dass die Aufrechterhaltung einer gleichmäßigen Mischung von Futterarten ebenfalls helfen kann, die Unkräuter zu unterdrücken.
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Introduction

Invasive weeds in pastures reduce forage quality and yield, impair animal performance, and increase management costs associated with herbicide application and pasture renovation (DiTomaso, 2000). A way to reduce weed abundance in pastures may include maintaining diverse assemblages of resident forage plants. Many experiments have reported reduced weed abundance with greater resident plant diversity in grasslands (Knops et al., 1999; Hector, Dobson, Minns, Bazeley-White, & Lawton, 2001; Pfisterer, Joshi, Schmid, & Fischer, 2004). A reduction of weed abundance in diverse plant communities may occur by two general mechanisms (Wardle, 2001) (1) 'Resource use complementarity', where the different species in a community complement each other in their resource use and create a strong competitive environment that is difficult for weedy plants to invade, and (2) the 'sampling effect' caused by the increased probability that a more diverse community will have at least one productive species that reduces available resources and suppresses weed abundance. Resource complementarity is a true 'diversity effect' in that interactions among multiple species in a diverse community help suppress weeds. The sampling effect is not a true diversity effect since weed suppression results from a strong competitive environment created by one species, not the interaction among multiple species.

Increased vegetation diversity may have other indirect beneficial effects on agroecosystems. For example, increased vegetational diversity can lead to suppression of pests via 'top-down' enhancement of natural enemy populations or by resource concentration and other 'bottom-up' effects acting directly on pests (Gurr, Wratten, & Luna, 2003). Similarly, Knops et al. (1999) found reduced leaf pathogen abundance with greater plant diversity in grassland plots. Some studies also suggest there may be tighter nitrogen cycling and less nitrate leaching with increased diversity in grasslands (Tilman, Wedin, & Knops, 1996; Scherer–Lorenzen, Palmborg, Prinz, & Schulze, 2003). Overall, maintaining diversity in agroecosystems may help improve crop yield or quality and increase the sustainability of the farming system.

The objective of this study was to determine whether increased forage plant diversity was associated with reduced weed abundance in the aboveground vegetation and in the soil seed bank of pastures grazed by cattle. We evaluated the soil seed bank because the quantity of viable weed seeds in soil represents a potential pool of invading species that could establish into the aboveground vegetation. Diverse pasture communities may indirectly affect the amount of weed seeds that accumulate in soil by suppressing weed invasion into pastures. Since most annual weed species have long-lived seeds, management strategies, like maintaining high-resident plant diversity, may help reduce the accumulation of these seeds and prevent potential weed problems in the future.

Materials and methods

Weed abundance and weed seed in soil seed banks were evaluated from a grazing experiment established in 1994 at the University of Missouri, Forage Systems Research Center located in Linneus, Missouri, USA. The experiment consisted of 15 grass or grass–legume mixtures that were established in a completely randomized design with 64 plots. All pasture mixtures planted included either *Festuca arundinacea* Schreb. or *Bromus inermis* Leysser in combination with various grasses and legumes (Table 1). *F. arundinacea* and *B. inermis* were chosen as base species for the mixtures because they are two of the most common pasture grasses used throughout much of the Midwestern, USA. Each pasture mixture was seeded to achieve a target rate of ~800 seeds m^{-2}. Monoculture pastures consisted of the base grasses, either *F. arundinacea* or *B. inermis*, each sown at 800 seeds m^{-2}. Two species mixtures contained each grass base paired with three different legumes (Table 1). The two species mixtures were sown at 400 seeds m^{-2} for each component. The three species mixture contained each grass base sown at 400 seeds m^{-2} in combination with two legumes sown at 200 seeds m^{-2}, respectively. The four species mix contained each grass base species with all three legumes sown in equal proportion (200 seeds m^{-2}). The six species mixtures contained each base grass, all three legumes, plus *Dactylis glomerata* and *Phleum pratense* sown in equal proportion. The eight species mixtures were the same as the six species mixtures except they contained both base grasses and *Andropogon gerardii* all sown in equal proportions. Plot size was 15 m × 15 m. Fourteen of the 15 mixtures had four replications while the eight species mixture actually had eight replications since the mixture contained both base grasses. Grasses were sown in September 1994 to a prepared seedbed. Legumes were frost seeded into grass mixtures in March 1995. In 1996 and 1997, plots were mechanically harvested approximately every 2 weeks from mid-May to mid-July. Beginning in 1998 and extending to 2002, individual plots were grazed by beef steers whenever mean sward height reached 20–25 cm. Plots were grazed by six steers for 4–7 h until they removed approximately 50% of the forage biomass. The grazing season lasted from April to November each year.

Soil sample collections for seed bank analysis were taken in June 1999 and at the end of the experiment in November 2002. Twenty soil samples (diameter 2.54 cm) were taken from random locations in each plot to a depth of 5 cm. Approximately 500 cm^3 of soil was removed from each plot. The surface area of soil removed was used to scale up seed number to m^{-2} basis. Soil samples were then frozen and shipped to the University of Illinois, Urbana, IL. Soils were stored at 0 °C in the dark.

Table 1. Pasture mixtures sown in grazing experiment at Linneus, Missouri, USA

Plant Species	Mixtures							
	1[a]	2	3	4	5	6	7	8[b]
Grass Base	x	x	x	x	x	x	x	x
Medicago sativa (L.)Alfalfa		x			x	x	x	x
Lotus corniculatus (L.) Birdsfoot trefoil			x		x	x	x	x
Trifolium pratense (L.) Red clover				x		x	x	x
Dactylis glomerata (L.) Orchardgrass							x	x
Phleum pratense (L.) Timothy							x	x
Andropogon gerardii (Vitman) Big bluestem								x

A total of 16 different mixtures were planted using eight mixtures each constructed with either *F. arundinacea* or *B. inermis* forming the grass base.

[a]Mixture 1 contained *F. arundinacea* or *B. inermis* in monoculture fertilized with 108 kg N ha^{-1} .

[b]Mixture 8 includes both *F. arundinacea* and *B. inermis*.

Soils collected in 1999 were stored frozen for approximately 6 months while soils collected in 2002 were stored for 3 months before gemination. Soils were thawed, air dried and spread into $25\,cm \times 50\,cm \times 6\,cm$ plastic trays to a depth of $\sim$1 cm over sterile potting soil. Trays containing the soil were placed in a greenhouse under natural light conditions. In both years, germination trials were conducted during the winter. Temperatures in the greenhouse ranged from 13 to 23 °C with a mean of 18 °C during the germination period. Trays were watered regularly and as seedlings emerged they were identified and removed from the trays. Germination trials were stopped after 8 weeks as the number of germinating species approached zero.

Aboveground species composition of the plots was taken each month of the growing season (April–November) in 1999 and 2002 using a point step method. Within each plot, plant species or other material contacted by the point at soil surface level was recorded on 10 transects consisting of 10 equidistant step points each. Point of contact was at ground level. The point used was the head of a #6 finishing nail which is approximately 2.5 mm. The nail was driven into the end of a square yardstick with about 3 cm extending from the square stick. The abundance of each species was calculated based on the number of step point contacts per species. Mean species abundance in each plot was calculated by averaging the number of contacts for each species over the growing season (May–October). For example, if one species averaged five step contacts over the growing season, it indicates that the species made up about 5% of the species composition (5/100 step points) in that plot.

To reduce subjectivity in classifying weed plants, we considered weeds any species that was not included in the original sown mixture. We recognize that some potentially desirable forage species may be considered 'weeds' using this classification. The species diversity of sown species was measured using several indices: species richness (S), Shannon–Wiener diversity index and species evenness (J). Species richness (S) was the number of sown forage species present in each plot. The Shannon–Wiener diversity index is calculated by $H' = -\sum(p_i)\ (\log_2 p_i)$ where p being the proportional relative abundance of forage species belonging to the ith species (Magurran, 1988). An index of forage species evenness (J) was calculated by dividing the Shannon index (H') by (H' max), which is the natural log (ln) of forage species richness (Magurran, 1988). Most weeds were not identified to species, so were excluded from the diversity calculations.

Simple linear regression was used to determine relationships between aboveground species diversity and weed abundance in the aboveground vegetation and soil seed bank. Differences in seed bank size due to primary pasture species mixtures, either *F. arundinacea* or *B. inermis*, was tested using one-way ANOVA. A paired t-test was used to test for differences in *F. arundinacea* and *B. inermis* abundance between 1999 and 2002. For all analyses we considered significance at $P < 0.05$.

Results

The species originally sown in 1994 accounted for 54% and 57% of step points of *F. arundinacea* and *B. inermis* pasture communities in 1999. The majority of remaining aboveground species included *Poa pratensis* L., *Lespedeza* spp., *Trifolium repens* L. and other weed species. Averaged across all mixtures, most sown species remained unchanged or increased slightly in aboveground abundance from 1999 to 2002. An exception was found in the *F. arundinacea* mixtures, where *F. arundinacea* significantly declined in abundance from a mean of 34 ± 2.7 step points per plot in 1999 to 28 ± 2.1 in 2002 (paired t-test, $P = 0.002$, df=7). *F. arundinacea* in the *B. inermis* mixtures increased significantly (paired t-test, $p = 0.02$, df=7) from 1999 to 2002.

The species composition of soil seed banks was similar in 1999 and 2002. We identified 46 species, and of those, 31 were found in both years of the survey (Table 2). *Digitaria ischaemum* was the most abundant seed bank species, averaging 318 ± 37 and 395 ± 61 seeds m^{-2} in 1999 and 2002. Other abundant seed bank species that appeared in both years included *P. pratensis* L., *Potentilla simplex* Michx., *Veronica peregrina* L., *Capsella bursa-pastoris* L. Medikus, and *Panicum capillare* L.. Of the originally sown species, only *Trifolium pratense* L. was found in sufficient quantity in the seed bank (3.7 and 6.0 seeds m^{-2} in 1999 and 2002, respectively).

In both years, aboveground weed abundance was unrelated to species richness (S) and Shannon–Wiener diversity index (H') of sown forage species (linear regression, $P > 0.05$). When the species evenness of sown forages (J) was taken into account, however, we found a significant negative relationship with weed abundance in both years (Fig. 1). Weed seed abundance in the soil was positively related to aboveground forage species richness in 1999 ($r^2 = 0.09$, $P = 0.01$, df=1, 62), but not in 2002 ($P > 0.05$). Diversity indices (H') and (J)

Table 2. Plant species identified from soil seed banks in 1999 and 2002

Species	1999		2002	
	Seed m^{-2}	Rel. abun.	Seed m^{-2}	Rel. abun.
Acalypha virginica L.	0.9±0.3	0.1	5.5±2.1	0.5
Amaranthus retroflexus L.	1.0±0.4	0.1	–	–
Ambrosia artemisiifolia L.	0.1±0.1	0.01	–	–
Anthemis cotula L.	–	–	0.5±0.5	0.04
Bromus inermus Leysser.	0.3±0.2	0.03	–	–
Capsella bursa-pastoris (L.) Medikus.	213.2±16.8	22.6	72.7±12.1	6.4
Cardamine parviflora L.	6.2±0.9	0.7	5.5±1.8	0.5
Cerastium arvense L.	1.9±0.6	0.2	2.5±1.3	0.2
Chenopodium album L.	0.3±0.2	0.03	3.5±1.3	0.3
Conyza canadensis (L.) Cronq	–	–	14.4±3.2	1.3
Cyperus spp. L.	2.1±0.7	0.2	10.0±2.2	0.1
Digitaria filiformis (L.) Koeler	11.6±2.4	1.2	4.5±1.6	0.4
Digitaria ischaemum (Schreber) Muhl.	318.5±37.4	33.8	395.1±61.8	35
Echinochloa crus-galli (L.) P.Beauv.	28.2±3.8	3	13.9±2.9	1.2
Erechtites hieraciifolia (L.) Raf.	0.1±0.1	0.01	–	–
Erigeron annuus (L.) Pers	12.7±1.7	1.3	–	–
Euphorbia maculata L.	1.6±0.6	0.2	6.0±1.9	0.5
Galium mollugo L.	0.3±0.2	0.03	0.5±0.5	0.04
Geranium carolinianum L.	–	–	0.5±0.5	0.04
Lamium amplexicaule L.	9.9±2.4	1.1	2.5±1.1	0.2
Lepidium campestre (L.) R.Br.	0.1±0.1	0.01	–	–
Lotus corniculatus L.	1.1±0.1	0.1	1.0±0.7	0.1
Medicago lupulina L.	–	–	0.5±0.5	0.04
Oxalis stricta L.	7.9±1.3	0.8	1.5±0.9	0.1
Panicum capillare L.	48.8±6.7	5.2	24.9±3.8	2.2
Panicum dichotomiflorum Michx.	3.1±0.6	0.3	–	–
Plantago lanceolata L.	–	–	3.0±1.2	0.3
Plantago major L.	8.3±2.3	0.9	108.0±17.2	9.6
Poa pratensis L.	117.3±12.8	12.4	50.8±9.8	4.5
Polygonum aviculare L.	0.3±0.2	0.03	–	–
Polygonum pensylvanicum L.	0.3±0.2	0.03	1.0±0.7	0.1
Portulaca oleracea L.	1.5±1.4	0.2	–	–
Potentilla simplex Michx.	36.2±3.6	3.8	39.3±5.9	3.5
Rumex obtusifolius L.	9.1±1.6	1	10.9±2.5	1
Setaria faberi R. Herrm.	0.9±0.6	0.09	1.0±1.0	0.1
Setaria glauca (L.) P.Beauv.	11.2±1.7	1.2	2.5±1.1	0.2
Solanum nigrum L.	0.4±0.04	0.04	3.0±1.5	0.3
Taraxacum officinale Weber ex Wiggers	3.6±0.9	0.4	29.4±8.7	2.6
Thlaspi arvense L.	1.7±1.2	0.2	2.0±1.2	0.2
Trifolium dubium Sibth.	1.2±0.5	0.1	7.0±2.2	0.6
Trifolium pratense L.	3.7±0.9	0.4	6.00±1.9	0.5
Trifolium repens L.	2.5±1.1	0.3	11.4±2.3	1
Verbena hastata L.	0.8±0.3	0.1	–	–
Veronica arvensis L.	5.7±1.5	0.6	5.0±1.9	0.4
Veronica peregrina L.	67.9±6.1	7.2	246.3±14.2	21.8
Veronica spp. L.	0.1±0.1	0.01	37.3±5.1	3.3

Values are expressed as germinable seed m^{-2} averaged across all 64 plots ±1SE. Relative abundance (Rel. abund.). refers to the abundance of each species stated as a percentage of the total species identified.

of sown forages were unrelated to weed seed abundance. The primary species in each pasture mixture (*F. arundinacea* or *B. inermis*) was related to the amount of viable seed in the weed seed bank (Fig. 2). In 1999, mixtures with *F. arundinacea* had less germinable seed than the *B. inermis* mixtures (one-way ANOVA, F=9.4, $P = 0.003$, df=1, 62). We found no statistical difference between these variables in 2002 ($P = 0.78$). Trends in the seed bank were also reflected in the aboveground

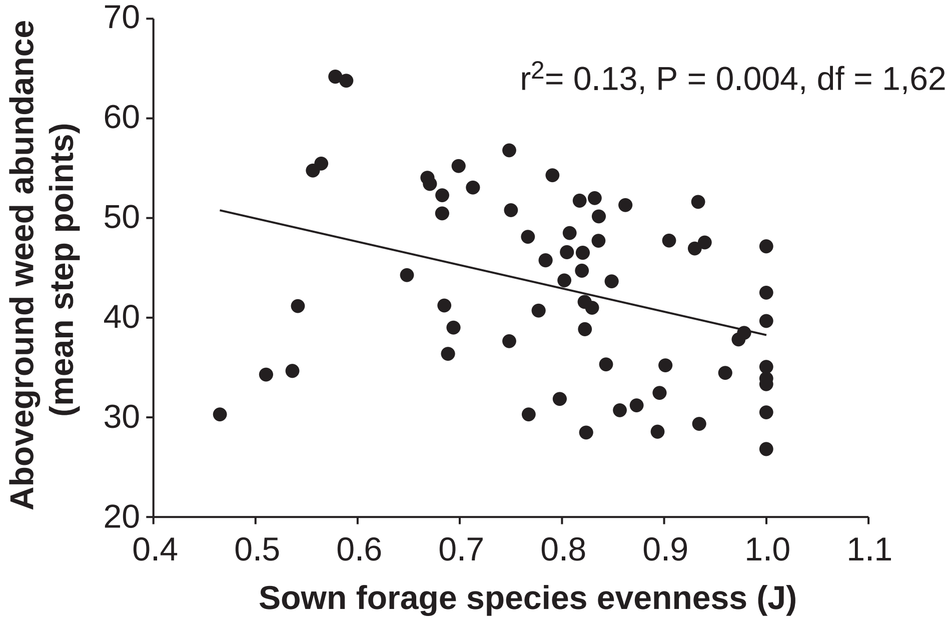

Figure 1. Relationship between aboveground weed abundance and forage species evenness (*J*). Weed abundance was calculated from mean step points per plot. Data points are averages between 1999 and 2002.

vegetation as mixtures with *F. arundinacea* had significantly less weed biomass (mean 30 ± 1.7 step points) than *B. inermis* mixtures (44 ± 2.2 step points) in 1999 (one-way ANOVA, F=24.4, $P = 0.0002$, df=1, 62). No significant differences in aboveground weed abundance were found in 2002.

Discussion

Results from this study suggest that the evenness at which forage species are distributed in pastures may help reduce aboveground weed abundance. Other recent studies also provide evidence that resident plant evenness may be important in suppressing weed invasion into grassland communities (Wilsey & Polley, 2002; Tracy & Sanderson, 2003). Diversity measurements generally take into account both the number of species (*S*) and how evenly (*J*) they are distributed in a community (Magurran, 1988). The findings here suggest that the evenness at which forage species are distributed within a pasture may be a more important predictor of weed abundance within pastures. Possibly, species that are evenly distributed in space may use resources more equitably and produce a competitive environment that is difficult for weeds to invade (Lyons & Schwartz, 2001; Wilsey & Potvin, 2000; Wilsey & Polley, 2002). Of course, other factors like forage productivity, soil disturbance, soil fertility, and propagule supply may also affect weed abundance at pasture scales (Smith & Knapp, 2001). In particular, highly productive communities may be effective at suppressing weeds. In our study, however, it seems unlikely that the productivity of the mixtures greatly contributed to the negative relationship between weed abundance and forage evenness. Forage dry matter yields were generally similar across mixtures of differing diversity both in 1998 and 1999, a year when growing season precipitation was 40% of normal (J. Gerrish, unpubl. data). Nevertheless, a combination of factors likely contributed to the high variation in weed abundance we found among plots (Fig. 1). Of these factors, forage species evenness appears to be important in explaining some of the variation in weed abundance.

Although many studies have evaluated relationships between resident plant community diversity and weed abundance, less is known about how this diversity may affect weed seed accumulation in soil. Although the diversity of mixtures did not appear to influence weed seed abundance, the species composition of pasture mixtures may have affected the size of soil seed banks. In 1999, the germinable soil seed bank of weeds under *F. arundinacea* mixtures was approximately 30% smaller than that under *B. inermis* mixtures. The smaller weed seed bank may reflect a greater relative abundance of *F. arundinacea* in the mixtures relative to *B. inermis*. The greater

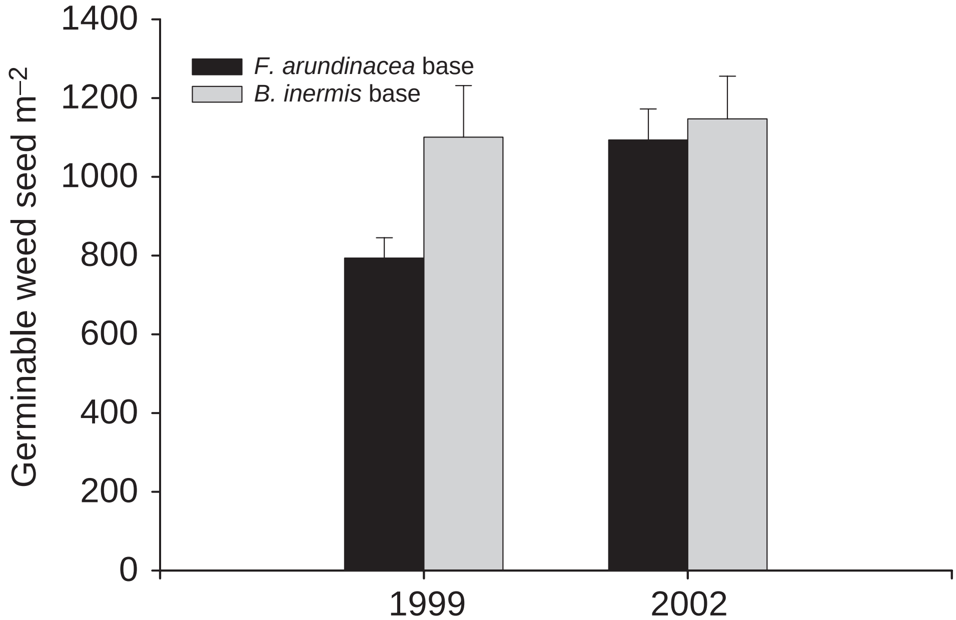

Figure 2. Germinable weed seed in *F. arundinacea* and *B. inermis* mixtures in 1999 and 2002. Bars are means ($\pm$1 SE) of the eight mixtures within each *F. arundinacea* and *B. inermis* mixture base.

coverage of *F. arundinacea* may have helped reduce weed abundance in many of these plots and thus resulted in less seed accumulation into the seed bank. Interestingly, as the relative abundance of *F. arundinacea* in the mixtures declined from 1999 to 2002, the size of the weed seed bank increased, and we found no difference between *F. arundinacea* and *B. inermis* mixtures in 2002 (Fig. 2). Trends in the seed bank were reflected in the aboveground vegetation as mixtures with *F. arundinacea* had significantly less weed biomass (30 ± 1.7) than *B. inermis* mixtures (44 ± 2.2) (one-way ANOVA, F=24.41, $P=0.0002$, df=1, 62). *F. arundinacea* was a dominant grass where it occurred in plots and it has been reported to be allelopathic to other plants (Smith & Martin, 1994; Chung & Miller, 1995; Renne, Rios, Fehmi, & Tracy, 2004). Competitive exclusion by *F. arundinacea* combined with its potential allelopathic effects may have helped reduce weed seed establishment and subsequent recruitment into the aboveground vegetation.

Findings from this study also support others showing that most sown grassland and pasture species do not develop large or persistent seed banks (McDonald, Bakker, & Vegelin, 1996; Akinola, Thompson, & Hillier, 1998; Tracy & Sanderson, 2000). Although sown forages may not persist in soil seed banks, our findings suggest that soil seed banks could be used to encourage the establishment of unconventional forages like *Digitaria* spp. In both years of the study, *D. ischaemum* dominated the composition of the soil seed banks. *Digitaria* spp. are warm season annual grasses that are typically considered weedy species in most grazing systems. Recruitment of *Digitaria* spp. into the aboveground vegetation, however, could add forage during hot summer months when cool season pasture mixtures tend to decline in productivity. Some ecotypes of *Digitaria* can provide productive, good-quality forage that may re-seed itself if managed properly (Voigt & Sharp, 1995; Dalrymple, 2000). *Digitaria* spp. were readily grazed by cattle through September in plots where it occurred suggesting that it was palatable and of good forage quality (J. Gerrish, pers. observ.). The persistence and large size of the *Digitaria* soil seed bank suggests that it could help provide summer forage to cattle if it were allowed to germinate and establish within the cool season mixtures.

Although factors like forage productivity, soil disturbance, soil fertility, and propagule supply affect weed abundance at pasture scales, our results suggest sowing or maintaining an evenly distributed array of forage plants should also help reduce weed abundance grassland communities.

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